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Risk and resilience in the late glacial: A case study from the western Mediterranean

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ABSTRACT

The period spanning the Last Glacial Maximum through early Holocene encompasses dramatic and rapid environmental changes that offered both increased risk and new opportunities to human populations of the Mediterranean zone. The regional effects of global climate change varied spatially with latitude, topography, and distance from a shifting coastline; and human adaptations to these changes played out at these regional scales. To better understand the spatial and temporal dynamics of climate change and human social-ecological-technological systems (or SETS) during the transition from full glacial to interglacial, we carried out a meta-analysis of archaeological and paleoenvironmental datasets across the western Mediterranean region. We compiled information on prehistoric technology, land-use, and hunting strategies from 291 archaeological assemblages, recovered from 122 sites extending from southern Spain, through Mediterranean France, to northern and peninsular Italy, as well as 2,386 radiocarbon dates from across this region. We combine these data on human ecological dynamics with paleoenvironmental information derived from global climate models, proxy data, and estimates of coastlines modeled from sea level estimates and digital terrain. The LGM represents an ecologically predictable period for over much of the western Mediterranean, while the remainder of the Pleistocene was increasingly unpredictable, making it a period of increased ecological risk for hunter-gatherers. In response to increasing spatial and temporal uncertainty, hunter-gatherers reorganized different constituents of their SETS, allowing regional populations to adapt to these conditions up to a point. Beyond this threshold, rapid environmental change resulted in significant demographic change in Mediterranean hunter-gatherer populations.

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1. Introduction

When most people think about glacial periods, they imagine a time of environmental hardship; Europe in the Upper Pleistocene is envisioned as a cold and forbidding landscape. Interglacials, conversely, are thought of as representing intervals of better conditions, when conditions were 'milder' and climate 'ameliorated'. From this perspective, the Last Glacial Maximum (LGM) was the interval when Europe and the rest of the world experienced environments most hostile to humanity; after this, conditions gradually improved until we reached the maximally favorable Holocene Interglacial (Richerson and Boyd, 2001). Yet it was while the Earth was in the Upper Pleistocene 'Ice Age' that our species extended its range over all of the world. It is under full glacial conditions that we see evidence for larger group size, more complex technologies, more sophisticated social organization, and more highly developed artistic expression by human hunter-gatherers in Europe than at any time prior to or afterwards—including in the Holocene. Indeed, on the basis of the archaeological record, there is every reason to believe that human populations of Europe were well adapted to living under glacial conditions and highly successful—and may even have been actively managing ecosystems to increase their ability to sustain them (Kaplan et al., 2016). In contrast, human

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groups in the initial millennia of the more 'favorable' Holocene seem to have been smaller, more dispersed, with less 'sophisticated' technologies and less symbolic expression in art. These discrepancies suggest that systematic reassessment of human ecology and environmental contexts would be useful for the transition from the glacial conditions that were 'normal' for most of the history of modern *Homo sapiens* to the interglacial conditions that we take for granted today.

Across the Northern Hemisphere, and for Europe in particular, this transition entailed the retreat of continental ice sheets and warmer temperatures of course. But it also meant increasingly severe ecological disruption. Global warming did not happen gradually as the Pleistocene drew to a close. Very rapid and extreme warming of the Bølling-Allerød Interstadial was followed by sharply colder oscillations returning to fully glacial temperatures in the Younger Dryas; these were followed in turn by even more rapid and severe global warming at the beginning of the Holocene (Clark et al., 2012; Lotter et al., 2012). Average global temperatures rose by as much as 6 °C, and so rapidly that they occurred within the span of human memory (Steffensen et al., 2008)—with equally significant changes in the amount and annual distribution of precipitation.

Plant community composition and species associations changed dramatically across Europe, with the spread of closed canopy deciduous forest at the expense of cool/cold savannah and steppe being the most notable consequence (Ammann et al., 2013; Kaplan et al., 2016). Of course, such significant reorganization in plant communities had a profound impact on the animals that depended on them. Large, herd-dwelling herbivores occupied the open vegetation communities that dominated Europe during the Upper Pleistocene, including elephants, rhinoceros, horse, saiga, and reindeer. In the Holocene Interglacial, they were replaced by forest-adapted game species (e.g., red deer, roe deer, aurochs, wisent) who roamed singly or in small groups.

There were equally severe impacts on coastlines. From the Pleniglacial to the early Holocene, sea level rose by nearly 300 m, inundating tens of thousands of square kilometers of continental shelf in Europe (Siddall et al., 2003; Lambeck et al., 2004; Clark et al., 2009). Simultaneously, rapidly melting ice sheets dumped enormous quantities of fresh water into the north Atlantic, altering thermohaline circulation patterns (Beveridge et al., 1995; Keigwin and Boyle, 2000). The loss of direct access to deep water resources of the continental slope as sea level rose and the shift of cold currents away from the European continent significantly decreased easy access to rich marine resources. From the point of view of these highly successful human populations so well-adapted to a glacial world, the rapid and extreme climate oscillations, sea level rise, and complete reorganization of plant and animal communities that marked the transition to Holocene conditions must have been an eco-catastrophe.

We seek to better understand the long-term consequences of the transition from glacial to interglacial environments for social-ecological-technological systems (SETS) in the western Mediterranean through a scientific assessment of environmental risk and human resilience, and their variable expression in space and time across this region. Prior to the modern, post-industrial era, this is the only time culturally and biologically modern humans have faced such rapid, significant global warming, and its environmental consequences, on a global scale. While hunter-gatherer bands are socially very different than today's urbanized world, this is our only opportunity to assess successful and unsuccessful strategies humans employed in dealing with the multidimensional impacts of such profound global change. Of additional importance is the fact that one set of strategies for adapting to the interglacial conditions of the Holocene was through greatly expanding and intensifying practices for managing 'natural' ecosystems. These practices—which include farming, herding, and forestry—initiated a suite of positive feedbacks that led to the modern urbanized world dominated by tightly coupled socio-natural landscapes whose dynamics are driven as much by human actions as biophysical processes (Ellis et al., 2013).

2. Methods

2.1. Issues for studying long-term change in socio-ecological-technological systems

Archaeology has a unique potential to coordinate interdisciplinary research on long term change in socio-ecological-technological systems (or SETS) (van der Leeuw and Redman, 2002; Redman et al., 2004; Redman, 2007; Ellis, 2015). Realizing this potential is challenging, however. Empirical evidence for prehistoric SETS is in the form of proxies that are static, material residues of dynamic biophysical processes and human decisions and actions. Additionally, it is necessary to synthesize paleoenvironmental and archaeological data that can take very different forms, are produced at very different scales, and are captured in very different formats. Moreover, relevant social and ecological dynamics interacted in complex ways, and were time and space transgressive at multiple scales.

To further complicate matters, the archaeological and paleoecological records are sparse and fragmentary, and relationships between the data that we can study and past socio-ecological-technological processes are far from straightforward. In most cases, proxies are preserved in sedimentary deposits where they have accumulated into time-averaged palimpsests of variable duration. And they are usually altered from their original condition and spatio-temporal organization to varying degrees by human and natural formation processes. Hence, the proxy record is much more coarse grained than the social and ecological dynamics we seek to understand.

To address these issues with the nature of the record of ancient SETS, we take a regional approach, and scale our analyses and interpretations to better match that of available data. To do this, we carry out a multi-disciplinary, multi-scale meta-analysis that builds on data collected in numerous prior research projects. The geographic region of interest for this meta-analysis encompasses the arc of the entirety of western Mediterranean Europe in the broad sense, including all of modern Italy, southern France, and Mediterranean Spain. This region spans diverse landscapes from Alpine zones to the warmest and driest areas of southern Europe, representative of much of the socio-ecological variation of late Glacial Europe beyond the periglacial zones.

We integrate new digital terrain models and results of recent, process-based paleoclimate simulations to complement this large, archaeological dataset. Our analyses employ data science methods anchored in conceptual frameworks of human behavioral ecology and lithic technology theory. We calculate quantitative measures of paleoenvironmental conditions and their spatial/temporal variability across the western Mediterranean, with a focus on measuring change, stability, and uncertainty. We also calculate measures of how SETS responded to environmental change and uncertainty, including metrics for land-use strategies and resource acquisition. Because of the issues discussed above, we emphasize shifts in long term strategies for SETS rather than short term tactics of hunter-gatherer societies.

2.2. Data sources: Terrain

We combine new digital terrain datasets, digital bathymetric

datasets, and estimates of late Pleistocene through early Holocene sea levels to construct models of paleolandscapes in the western Mediterranean. For terrestrial terrain, we use the EarthEnv 90 m DEM (digital elevation model) that merges the CGIAR-CSI SRTM (shuttle radar topography mission) v. 4.1 and Terra/ASTER GDEM v. 2 data products (Robinson et al., 2014). This is a global, high-resolution, high-accuracy, representation of modern terrestrial topography. However, lowered sea levels during the last glaciation exposed the continental shelves, changing coastlines and significantly expanding land areas. To represent these changes in western Mediterranean landscape and coasts, we merged the EarthEnv DEM product with the GEBCO (General Bathymetric Chart of the Oceans) Bathymetric dataset (Weatherall et al., 2015). Because this new global DEM of the ocean floor has a 30 arc second resolution, we downscaled it to 90 m, using spline-based interpolation methods to match the EarthEnv DEM.

To create digital models of the late Pleistocen and early Holocene landscape, we then added the amount of sea level lowering estimated for multiple chronological periods (based on Siddall et al., 2003) to each cell of the merged terrestrial/bathymetric DEM. For example, LGM sea level is estimated to have been an average of 106 m below current mean sea level. By adding 106 to the elevation of each cell in our DEM, a coastal cell with a current elevation of 0 m amsl, is transformed into an inland LGM locale with an elevation of 106 m amsl, and a seafloor cell with a modern elevation of 106 m below mean sea level becomes a coastal site with an elevation of 0 m amsl. We repeated this procedure for each of four time periods used in this analysis (see below). We did not take into account the effects of crustal deformation due to ice sheet loading in northern Europe or regional neotectonics, both of which may have affected the position of paleocoastlines variably across space, as opposed to the simpler 'bathtub' method of estimating sea level changes we use here (Kaplan et al., 2016). There is no comprehensive data on Upper Pleistocene neotectonics for the western Mediterranean that we know of that would allow us to model its impact across the region. Peltier and colleagues (Argus et al., 2014; Peltier et al., 2015), on the other hand have created a global dataset on topographic anomalies due to ice sheet loading (Peltier, 2015). While this shows differences of up to several hundred meters above or below coastlines calculated by simply lowering global sea level for regions of northern Europe, near the ice sheet, their model indicates less than 10 m of variation across the western Mediterranean. Moreover, we calculate sea level means for chronological intervals used in this paper (see below and Table 1) rather than modeled values for particular points in time, and the temporal variation in global sea level across each of these periods is greater than the modeled spatial variation in the western Mediterranean due to crustal deformation caused by northern European ice sheets. These simple digital models of late Pleistocene/early Holocene terrain serve as a base layer for subsequent modeling of environmental variability.

2.3. Data sources: Paleoclimate

In order to acquire continuous coverage data in space and time for global climate change and its multi-dimensional manifestation in the western Mediterranean, we employ process-based paleoclimate modeling. Proxy paleoclimate data such as isotopic ratios extracted from speleothems and ocean cores, and microfaunal assemblages from sea cores, have been linked to global ice volume and sea surface temperature (Rasmussen et al., 2008). While they are an invaluable record of past global climate change (see Fig. 1), they are very sparse, point sources, and the information they provide often is not at the locations or scales (geographic or temporal) most relevant to understanding SETS responses to environmental change and uncertainty. The pollen record can help to reconstruct regional terrestrial vegetation, but deep pollen cores that extend back into the Upper Pleistocene are also rare point sources. Moreover, links between ancient vegetation communities and climate are often subjective and qualitative ("cold and dry" or "cool and moist"), and recent work (Kaplan et al., 2016) suggests that late Pleistocene vegetation communities of western Europe may have been significantly altered by human activities, calling into question their ability to serve as an unbiased paleoclimate proxy.

Paleoclimate models avoid the above limitations of paleoclimate proxies by using fluid-dynamics equations to simulate the response of atmospheric and oceanic circulation to processes such as solar insolation changes, biogeochemical cycling, and ice-sheet effects on albedo (Vertenstein et al., 2012; Otto-Bliesner et al., 2015). The best, current-generation models perform well when compared against the highest resolution global proxies (Liu et al., 2009; Prado et al., 2013). Importantly, climate models generate output for numerous climatological phenomena at time scales from hours to months. These processes-based climate models have limitations of their own, of course (Braconnot et al., 2012). Particularly relevant to this study, there are no publicly available results of paleoclimate simulations that span the entirety of the late Pleistocene through Holocene at high spatial resolution. Currently, there is one openly available global dataset, TraCE-21K (Liu et al., 2009; He, 2011; Otto-Bliesner et al., 2014), that spans the period from the Last Glacial Maximum to the present day (22,000 ka BP to 1990 CE) at monthly and decadal temporal resolution. TraCE-21K was generated by the Community Climate System model version 3 (CCSM3) (Liu et al., 2009). Because of the amount of processing needed to model the

Table 1
Chronological framework for organizing datasets. Sea level estimated from Siddall et al. (2003), dates calibrated with BChron, using Marine13 curve.

Period	Dates	Archaeological Lithic Industries	Sea Level
Initial Holocene	10-6 ka	Mesolithic, Sauveterian	−15 m mean Red Sea level for 10-5ka cal BP
End Glacial	14-10 ka	Late and Final Epigravettian, Epipaleolithic, Azilian, Final Magdalenian	−51 m mean Red Sea level for 14-10ka cal BP
Late Pleniglacial	19-14 ka	Badegoulian, Magdalenian (except Final), Epigravettian (except Late & Final), Tardigravettian, Salpêtrian (except Early), generic "Upper Paleolithic" from Tagliente	−84 m Red Sea level at 17ka cal BP (estimated by linear model because no empirical values available)
LGM	29-19 ka	Early Salpêtrian, generic "Upper Paleolithic" from Arena Candide, Early Gravettian from Grotte de la Cala	−106 m mean Red Sea level for 27-19ka cal BP

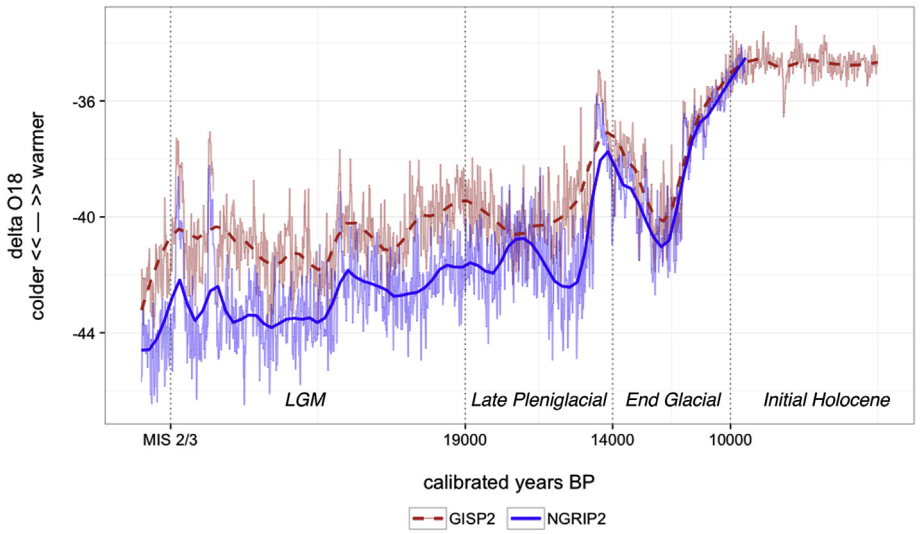

Fig. 1. Delta ^{18}O data from NGRIP2 and GISP2 ice cores with recalibrated dates for the period discussed in this paper. Based on data generated by (Rasmussen et al., 2008). Heavy lines are *locally weighted least squares regression* (LOESS) trends for the raw data (indicated by light lines).

Earth's atmosphere for 21,000 years at an original temporal resolution of 6 h intervals, a coarse spatial resolution of 3.75° was used (see Fig. 2). Multi-model ensembles of higher resolution (1°) simulations are also available for equilibrium time slices for the LGM (22ka BP) and mid-Holocene (6ka BP) (Braconnot and Kageyama, 2015). We use both sets of paleoclimate simulations (transient runs and equilibrium time slices) to look at temporal variability and uncertainty in several important climatic parameters across the entire span of time from the LGM to early Holocene in different parts of the western Mediterranean (TraCE-21K), and to compare spatial variability and uncertainty in climate between glacial and interglacial landscapes of this region (LGM and mid-Holocene ensembles). We statistically downscaled the LGM and mid-Holocene ensembles to a 10 km resolution more appropriate for understanding SETS dynamics, drawing on present-day climate and morpho-topographic information to minimize biases introduced by any particular ensemble member (Vrac et al., 2007; Supplementary Information S3; Gauthier, 2016).

2.4. Data sources: Prehistoric SETS

We cannot directly observe past human behavior, so we must rely on material residues of that behavior as proxies for SETS. Even hunter-gatherers have a rich technological repertoire and produce diverse waste products as a consequence of social practices. But most of this is lost to natural or anthropogenic post depositional destruction during the formation of the archaeological record. Moreover, modern methods archaeological data recovery like

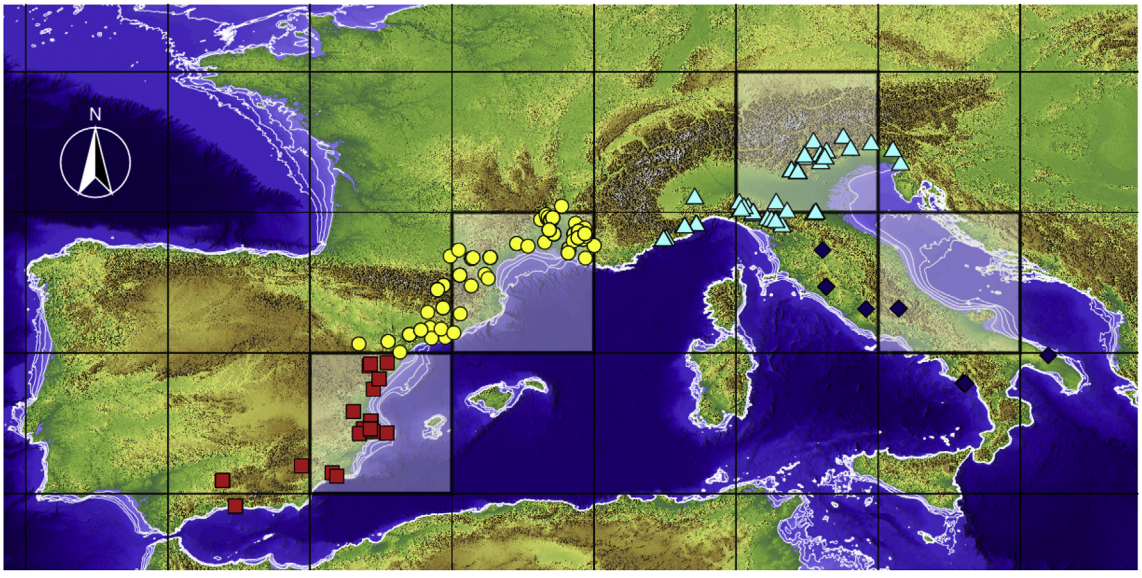

Fig. 2. Map of the western Mediterranean showing sites from which data discussed in this paper were drawn, colored according to the geographical subregions discussed in the text (red squares: Southwest subregion, yellow circles: North Central subregion, cyan triangles: Northeast subregion, dark blue diamonds: Southeast subregion. White coastal boundaries show the position of the coast line in the LGM, Late Pleniglacial, End Glacial, and Initial Holocene (see text and Table X). Black grid lines show TraCE21k paleoclimate grid cells and the four cells (light shading) used to characterize climatic change and uncertainty in the four geographic subregions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

micromorphology and 3D recording of artifact positions have only been applied to a small number of recently excavated sites. By far the most common and most commonly recovered material residues of human activity from the late Pleistocene and early Holocene are stone artifacts and their manufacturing debris (*lithic* artifacts), and hard parts of animals (bones, teeth, and shell)—from animals eaten, hard parts used as tools/ornaments, and from the skeletons of animals that lived and died in the same places that humans did but were not used by humans (e.g., small rodents).

Because our meta-analysis synthesizes multiple published sources, we focus our analyses on stone artifacts and animal bones as proxies for SETS. Fortunately, these offer important insights into dimensions of human ecology and land-use strategies that are important ways in which hunter-gatherer SETS respond to environmental change. We have compiled data from 291 archaeological assemblages, recovered from 122 archaeological sites across the western Mediterranean region. This represents a total of 527,118 lithic artifacts and 304,260 animal bones, with exemplars of most of the traditionally defined archaeological *industries* of the *Upper Paleolithic* (late Pleistocene) and *Mesolithic* (early Holocene) of western Europe (see Table 1). We also compiled proxy demographic data from 2,386 radiocarbon assays across this region. (See Supplementary Information S1 for list of all sites from which assemblages were drawn; all data analyzed for this paper and R Markdown scripts detailing all analyses are published and openly available at: https://github.com/cmbarton/Risk-Resilience_QSR2017/releases/tag/v1.0).

It is important to note that the great majority of the sites from which these data are drawn are caves and rockshelters. These locales probably are not representative of the majority of human settlements, but are by far the most common type of Upper Pleistocene archaeological site excavated and reported in the literature. As long-term landscape features, they attracted human occupants repeatedly and their sheltered environments preserved artifact bearing deposits, but they are obviously biased toward particular geological contexts while their constrained space and characteristic depositional environments favor the creation of palimpsest assemblages derived from multiple occupations (Barton and Clark, 1993).

2.5. Data integration

In order to model interactions between environmental uncertainty and resilience in SETS across the glacial/interglacial transition, we must combine the different datasets, originally compiled at quite different spatial and temporal resolutions and scales, into a common spatial/temporal framework. TraCE21k paleoclimate model output is available at monthly temporal resolution, or monthly averages by decade. We used the decadal averaged data because it has more manageable file sizes and still has a much higher temporal resolution than all other data used here. However, the TraCE21k data have a coarse spatial resolution. We did not downscale this model spatially, but rather looked at patterns of temporal change in four different geographic subregions we could characterize climatically on the basis of the 3.75° extents of the model grid cells (Fig. 2):

- a ***Southwest subregion*** spanning eastern and southern Mediterranean Spain,
- a ***North Central subregion*** that includes northeastern Mediterranean Spain and Mediterranean France,
- a ***Northeast subregion*** encompassing northern Italy, and
- a ***Southeast subregion*** representing peninsular Italy and geographically associated islands of Corsica, Sardinia, and Sicily.

We did downscale the 1° LGM and mid-Holocene time slice model ensembles to a 10 km spatial resolution. These procedures allow us to combine terrain and paleoclimate at different spatial and temporal resolutions.

We also analyzed archaeological assemblages within these four geographic subregions. This is a significant departure from the more common archaeological practice of grouping assemblages into named "industries" (e.g., *Solutrean* or *Badegoulian*) according to similarities in artifact forms. However, grouping assemblages by subregions that align with paleoclimate data gives us a consistent ecological framework in which to compare the human responses to environmental variation in space and time across the entirety of the western Mediterranean.

Archaeological sites were mapped as points, using published geographic coordinates (Fig. 2). Because 43% of the assemblages we use lack of numerical/radiometric dates, we grouped them temporally into four broad chronological periods: ***Last Glacial Maximum*** (LGM), ***Late Pleniglacial***, ***End Glacial***, and ***Initial Holocene*** (see Table 1 for details). Artifact and faunal assemblages were assigned to these periods on the basis of median calibrated ^{14}C ages where available, and by the broadly construed ages of techno/typological lithic industries where these radiometric were not available. All radiocarbon dates were calibrated using the BChron package in R and the Intercal13 (for terrestrial materials) or Marine13 (for marine shell) calibration curves (Parnell et al., 2011).

As described above, we downscaled the GEBCO bathymetry to 90 m and merged it with the EarthENV terrestrial DEM. We created temporal 'snapshots', based on sea levels calculated for each of the four temporal periods (see Table 1) to match the archaeological data with contemporaneous terrain across the study region.

3. Results

3.1. Ecological dynamics

Figs. 3–6 show different temporal and spatial dimensions of ecological change, and especially changes in environmental uncertainty (see Supplementary Information S3 for details of methods used). Figs. 3–5 compare data from paleoclimate model ensembles for the LGM and mid-Holocene across the entire west Mediterranean region. Unsurprisingly, mid-Holocene temperatures are warmer than the LGM in both winter and summer, with increases in summer temperatures more notable than winter temperatures (Fig. 3A). Precipitation change is more complex (Fig. 3B), although it decreases from the LGM to mid-Holocene in most parts of the region.

Changes in environmental uncertainty—and potential ecological risk for human inhabitants of this region—are less intuitive. At short, annual time scales, there an increase in seasonality of temperature (i.e., difference between summer and winter temperatures) from the LGM to the Holocene over all of the region (Fig. 4A). There is also increasing seasonality in precipitation in parts of Italy and France, little change in seasonality in other areas of Italy and France, and decreasing seasonality from the LGM to mid-Holocene over much of the Iberian portion of the region (Fig. 4B). This indicates an important spatial component to environmental uncertainty across the western Mediterranean.

We measured spatial uncertainty by calculating the standard deviation in temperature and precipitation within a 25 km moving window passed over the 5 km grid cells of this region for the downscaled from LGM and mid-Holocene time slice paleoclimate models (Fig. 5). Then we calculated maps of the difference in standard deviation between LGM and mid-Holocene (i.e., *anomaly* maps). Looking at the difference between the LGM and mid-Holocene, rather than the calculated values for each time slice,

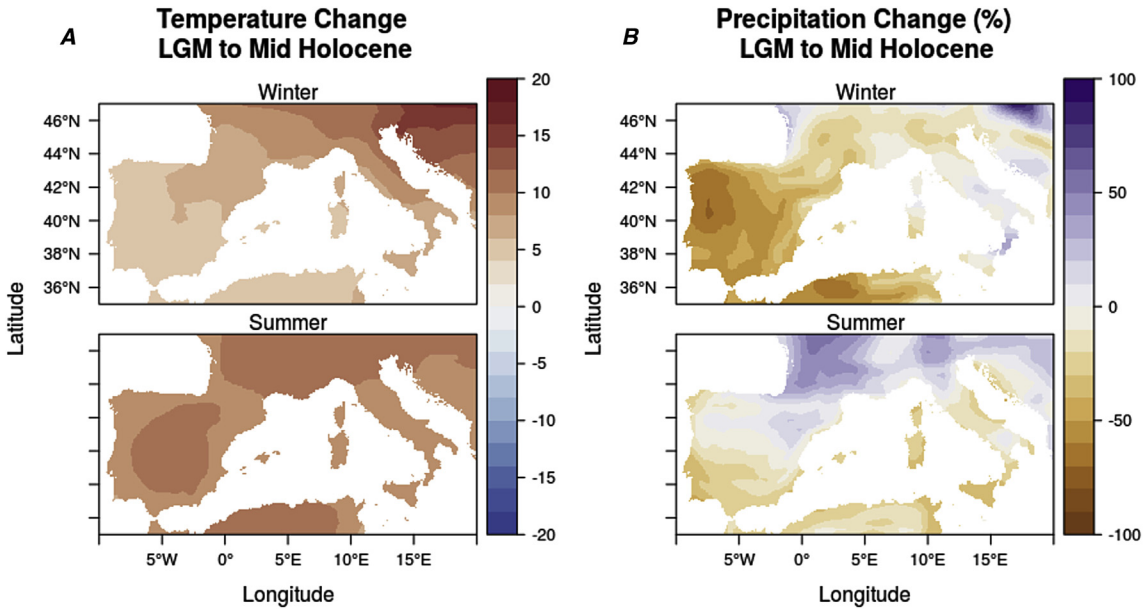

Fig. 3. Changes in annual temperature and precipitation from the LGM to mid-Holocene, based on CMIPS5 paleoclimate ensemble model output (see Supplementary Information S3 for procedures).

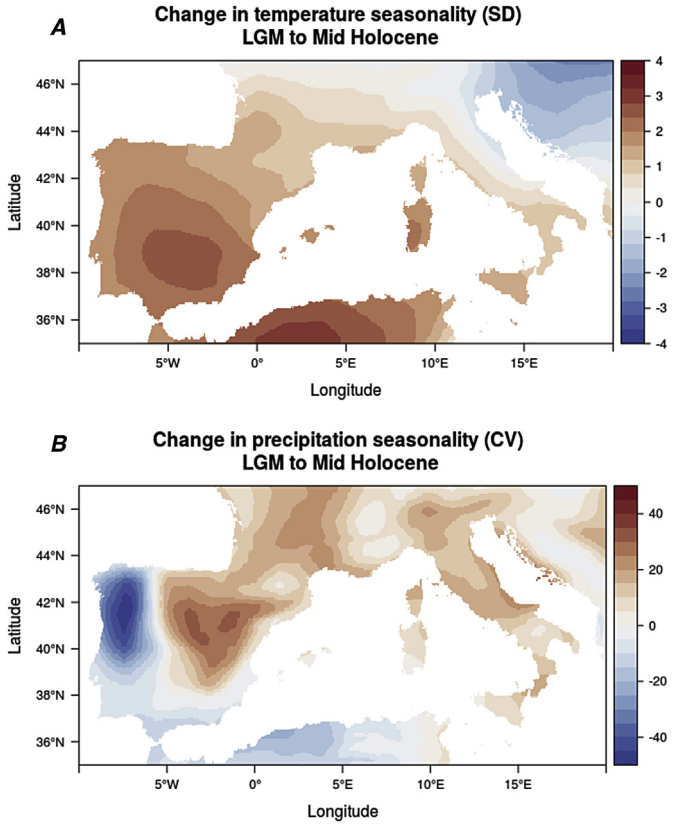

Fig. 4. Changes in temperature and precipitation seasonality from the LGM to mid-Holocene, based on CMIPS5 paleoclimate ensemble model output (see Supplementary Information S3 for procedures).

removes the effects of spatial heterogeneity due to topography alone, since the same topography underlies maps of both periods.

In essence, these maps show shifts in the ability of hunter-gatherers to predict environmental conditions across a foraging catchment given their knowledge of any location in that catchment. There is an increase in spatial heterogeneity of temperature (i.e., the landscape becomes less predictable from place to place) and decrease in spatial heterogeneity for precipitation (i.e., each locale is more like neighboring locales) for most parts of the western Mediterranean from the LGM to the mid-Holocene. Overall then, western Mediterranean environments become more seasonal and less predictable geographically with respect to temperature, and somewhat more predictable—though with variable change to seasonality—with respect to precipitation between the extremes of glacial and interglacial world climates.

These differences are borne out in analyses of temporally continuous paleoclimate trends, which also provide more detail in the shifting nature of ecological uncertainty through time in this region. Fig. 6 shows decadal means for total annual precipitation and mean annual temperature from 22-6ka, temporal trends (calculated using Empirical Mode Decomposition—see Supplementary Information S3), and the detrended variance for each of the four chronological periods used in the analysis here (Table 1). Detrended variance is a measure of the amount which decadal value deviates from the overall trend during a period, and indicates the ability to predict future conditions on the basis of past conditions. Based on this metric, the LGM exhibits the least environmental uncertainty of the three Pleistocene periods for both temperature and precipitation in three of the four subregions (the Late Pleniglacial has a slightly lower variance for mean annual temperatures in the Southeast subregion, and for annual precipitation in the Northeast subregion). The LGM is also exhibits better predictability for annual temperatures than even the Initial Holocene except in the Southeast subregion.

On the other hand, the Late Pleniglacial and especially the End Glacial periods exhibit much higher values for detrended variance than the LGM, indicating that these were times of increased environmental uncertainty and ecological risk than either the LGM or Initial Holocene. Below, we examine evidence for hunter-gatherer ecological behaviors from the environmentally stable LGM, through subsequent intervals of higher uncertainty, and into the (somewhat) more stable Initial Holocene.

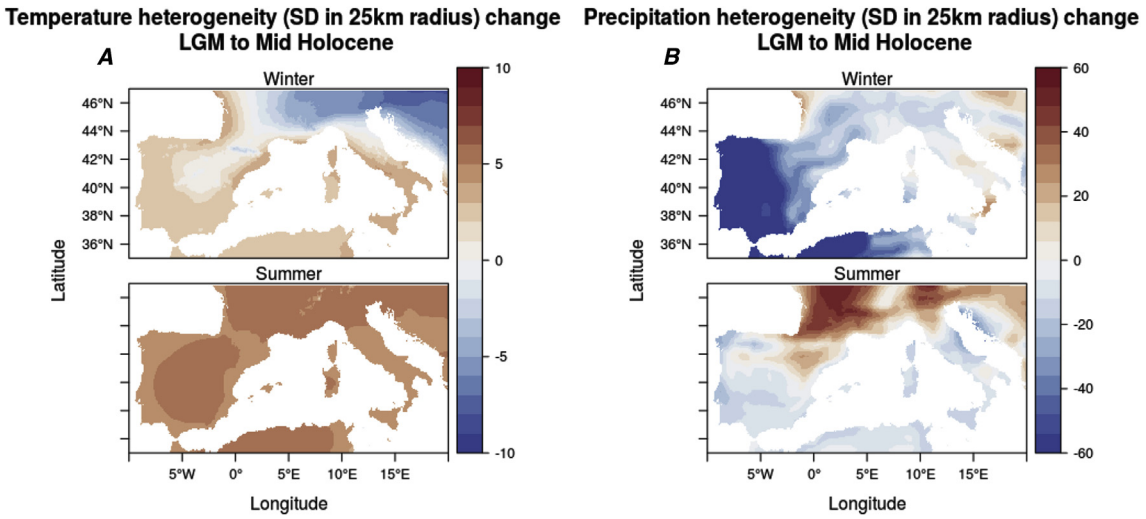

Fig. 5. Changes in spatial uncertainty for temperature and precipitation from the LGM to mid-Holocene, based on CMIPS5 paleoclimate ensemble model output (see Supplementary Information S3 for procedures). Only values above −60 are shown in 5B, preventing patterns from beyond the west Mediterranean from masking those in the study area.

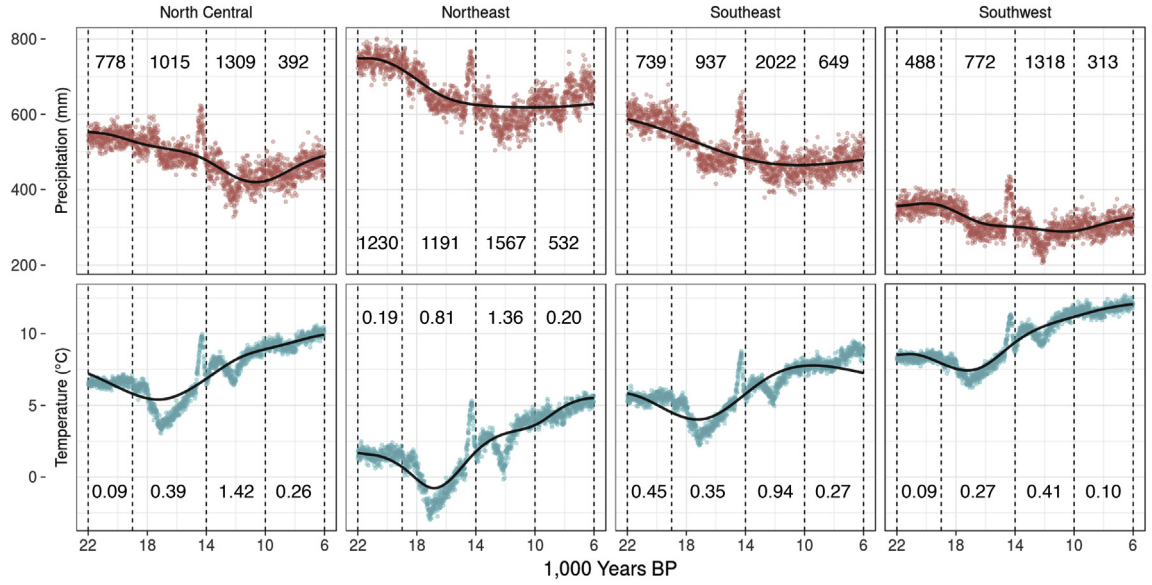

Fig. 6. TraCE21k modeled total annual precipitation and mean annual temperature for each of the four geographic subregions discussed. Black line is *empirical mode decomposition* (EMD) trend, and numbers indicate detrended variance for each of the four temporal periods discussed (see text and Supplementary Information S3).

3.2. SETS land-use strategies

A series of empirical and experimental studies has shown that variation in the frequency of edge modification (i.e., *retouch*) in assemblages of lithic artifacts is a robust proxy for hunter-gatherer land-use strategies (Riel-Salvatore and Barton, 2004, 2007; Barton et al., 2011, 2013; Barton and Riel-Salvatore, 2012, 2014). This simple, quantitative measure cross-cuts traditionally used classifications schemes based on (usually subjectively grouped) artifact morphology and whose meanings (e.g., social groupings, manufacturing traditions, different life histories, or functional tool kits) have spawned decades of debate. It can be applied consistently to all assemblages of the region regardless of the traditional classification schemes to which they were assigned in published reports.

Low values for *retouch* frequency are associated with dominant use of sites as logistical base camps, occupied for weeks or months, while high values for retouch frequency are indicative of assemblages primarily deposited during ephemeral occupations, either as a result of land-use characterized by residential mobility or when a site served as a camp for targeted resource extraction (e.g., hunting camp) by occupants of a logistical base camp elsewhere (Barton et al., 2013; Barton and Riel-Salvatore, 2014). Where sufficient data have been recorded, logistical base camps with assemblages having low retouch frequency are also associated with higher densities of overall lithic artifacts and debris, evidence of compound weapon manufacture (where and when such technology was in use), and relatively low frequencies of bones of large animals in faunal assemblages. Conversely, assemblages with high retouch frequencies, characteristic of ephemeral occupations are associated with lower total lithic densities, evidence of compound weapon maintenance, and higher frequencies of large animal bones (Neeley and Barton, 1994; Riel-Salvatore and Barton, 2004; Riel-Salvatore et al., 2008; Barton et al., 2013; Clark and Barton, 2017).

For the sites used in the meta-analysis here, we lack consistent, quantitative information about lithic density and compound weapon manufacture, but do have some data related to compound weapon maintenance. We also have sufficient information about faunal assemblages to calculate the *large herbivore index* (LHI)) for many assemblages. Similar to the *artiodactyl index* used in North America (Broughton, 1984; Szuter and Bayham, 1989; Schollmeyer and Driver, 2012), LHI = NISP (Number of Identified Specimens Present) of large mammalian herbivore remains divided by the combined NISP of large and small mammalian herbivores, where adult weight of 30 kg divides large and small herbivores (see also Supplementary Information S1).

As can be seen in Fig. 7A, there is a strong positive correlation between retouch frequency and LHI. Moreover, there is an equally strong correlation between the relative frequency of backed bladelets (discarded during compound tool maintenance) and LHI (Fig. 7B). In other words, among the assemblages analyzed here, those with higher retouch frequencies are also those with more evidence of compound weapon maintenance and higher incidence of large faunal remains, suggesting that they primarily accumulated during ephemeral occupations focused on large game hunting and butchering. Assemblages with low retouch frequencies, on the other hand, primarily accumulated during longer occupations at base camps, where large game were locally depleted and/or were hunted in long distance forays that favored field butchery (i.e., leaving bones at hunting camps) and returning to the base camp with meat that left few bones of these animals in site debris (see below and Barton et al., 2013).

Examining retouch frequencies of all assemblages by time period (Fig. 8), shows that most assemblages analyzed here accumulated when sites were occupied as logistical base camps. This is consistent with previous studies that have documented the dominance of logistical land-use strategies in western Eurasia during MIS 2 (Riel-Salvatore et al., 2008; Barton et al., 2011; Barton and Riel-Salvatore, 2016). Surprisingly, strongest evidence for a predominance of logistical base camps comes from the Holocene and End Glacial periods, with median values for retouch frequency of 0.10 and 0.11 respectively. However, median values for retouch frequency are only a little higher for LGM (0.14) and Late Pleniglacial (0.17) assemblages.

Notably, the two periods with the highest values for

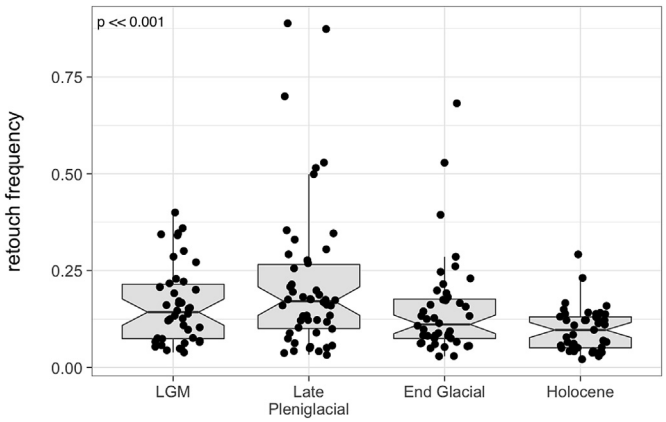

Fig. 8. Retouch frequencies for all assemblages by time period. Notches in box plots indicate 95% confidence intervals; p is for ANOVA.

environmental uncertainty (Late Pleniglacial and End Glacial) also display the greatest proportion of assemblages that accumulated in ephemeral camps rather than logistical base camps. While this could indicate that one response to increased environmental uncertainty and potential ecological risk was to shift to more residentially mobile land-use, sites with high retouch frequencies are associated with emphasis on large game. 80% of the sites with retouch frequencies ≥0.30 have *LHI* values above 0.5, suggesting that is more likely that these ephemeral occupations represented by assemblages with higher retouch frequencies represent hunting camps of logistically organized hunter-gatherers.

Decomposing retouch into the four subregions shows geographic differences in land-use across the LGM to Holocene time range (Fig. 9). There is statistically no change in land-use practices from the LGM into the Initial Holocene across the Southwest (eastern and southern Mediterranean Iberia) and Southeast (peninsular Italy) subregions. That is, increased environmental uncertainty during Late Pleniglacial and End Glacial, seems to have had minimal impact on hunter-gatherer land-use in these regions. This is consistent with previously reported evidence for the long-term stability of land-use in Mediterranean Iberia (Barton et al., 2013). It is the North Central (northeastern

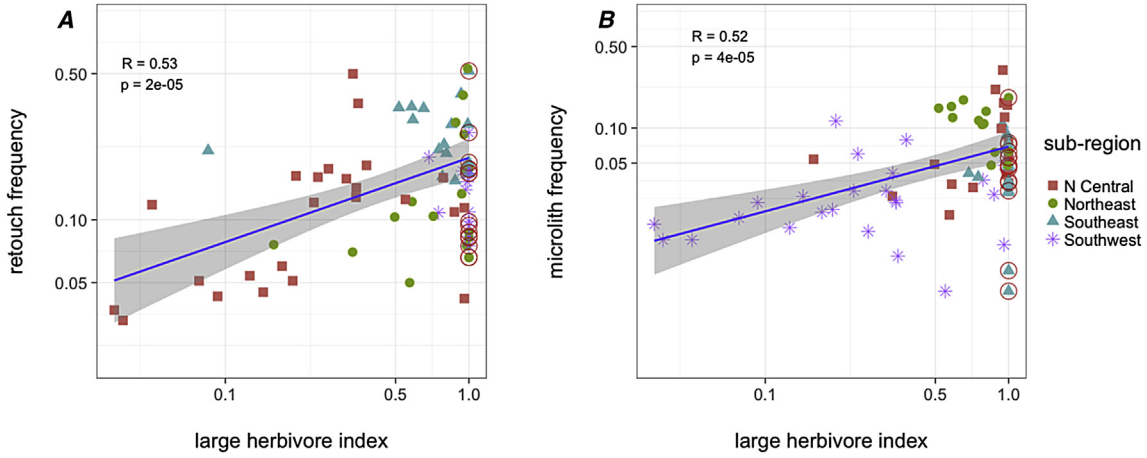

Fig. 7. A) Retouch frequency, as proxy for land-use, compared with large herbivore index (LHI) as a proxy for hunting/butchery practices among assemblages. Note log/log scales B) Microlith frequency, as proxy for compound weapon maintenance, compared with LHI. Marker shape and color show assemblages by geographic subregions. R and p are for simple linear regression indicated by blue line and 95% confidence interval grey shading. Circled points are assemblages with LHI = 1.0, and probably do not report small animals among the fauna (see text). Circled assemblages are excluded from regression statistics shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

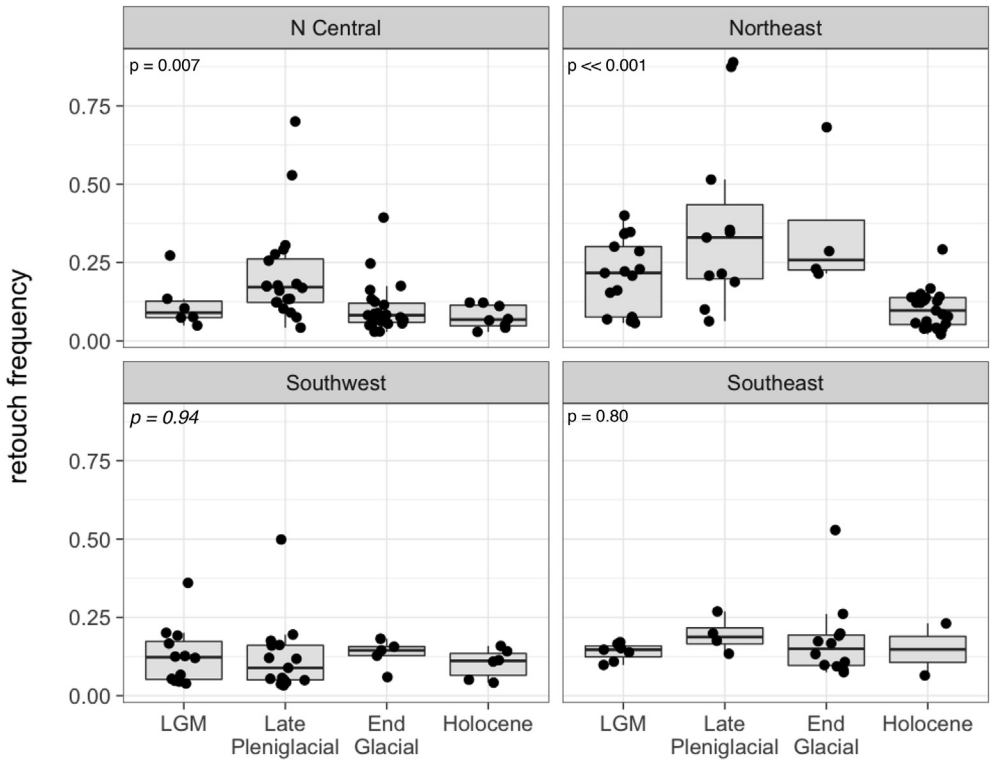

Fig. 9. Retouch frequencies for all assemblages in each subregion by time period. P values are for ANOVA calculated for each of the four plots.

Mediterranean Spain and Mediterranean France) and Northeast (northern Italy) regions that generate most of the variability in retouch frequency seen in Fig. 8. Both these northern Mediterranean regions show notable increases in the frequency of ephemeral camps during the Late Pleniglacial, and also in the End Glacial for the Northeast subregion.

If this is indeed evidence of sites being used more often as hunting camps (or ephemeral occupations for other targeted resource extraction) within an overall logistical land-use strategy, where are the 'missing' base camps following the LGM in the northern margin of the western Mediterranean? One possibility is that they are located on the continental shelf. Many of the sites in the North Central subregion and in the Northeast subregion border the Gulf of Lyon and Adriatic Sea, respectively, both of which have extensive continental shelf zones that would have been exposed during times of low sea level (Fig. 2). Sites in the Southeast and Southwest region border less extensive continental shelf areas.

Fig. 10 shows proxy data for land-use (i.e., retouch frequency) and hunting/butchering practices (i.e., LHI) relative to the distance from the coastline when each assemblages was accumulating. LOESS curves overlay assemblage points to show geographic trends. As noted in prior work (Barton et al., 2013), there is a general tendency for assemblages accumulating in base camps (i.e., lower retouch frequency and lower LHI) to predominate in a zone approximately 40–60 km from the contemporaneous coast. Ephemeral camps with higher retouch frequencies and higher LHI values are located both seaward of the base camps, in a zone 0–15 km from the coast, and further inland, at 100–125 km from the coast. If post-glacial sea level rise has inundated sites <60 km from Pleistocene coasts, other base camps and seaward ephemeral camps would now be under water. This is the case in the northern Adriatic (much of the Northeast subregion), where the coastline has retreated some 300 km from the LGM (Fig. 1) and around the Gulf of Lyon (part of North Central subregion) where the coastal retreat has exceeded 60 km. The coastline has retreated nearly 60 km in the northernmost part of the Southwest subregion, but much less over the rest of the subregion, and even less bordering the Southeast subregion. More detailed spatial analysis is needed, however, to evaluate this possibility.

3.3. SETS hunting strategies

Several aspects of hunter-gatherer hunting practices have been mentioned in the preceding discussion of land-use. One is variability in the emphasis on large vs. small game (at least with respect to faunal assemblages that accumulated at occupation sites). A second is a pattern of base camps, situated about 50 km inland from the coast, associated with ephemeral hunting camps located 40–50 km away in both seaward and landward directions—suggesting maximum territory extent of up to 100 km in diameter. A group of 73 assemblages from the French part of the North Central subregion have NISP counts of faunal taxa (Rillardon and Brugal, 2014) allowing more in-depth analyses Late Pleistocene to Early Holocene hunting patterns. Although these sites have been assigned to techno/typological industries (e.g., as in Table 1), complete counts of retouched and unretouched lithic artifacts have not been reported, unfortunately, preventing direct comparison of these detailed faunal analyses with proxies for land-use discussed above. Nevertheless, these data do provide valuable information about temporal change in human ecology for one subregion that is consistent with the results of analyses for all subregions of the western Mediterranean discussed above.

We calculated a standard measure of faunal diversity, the Inverse Simpson Index (also called Simpson Dominance Index), that combines information about richness and evenness into a single value that is robust to differences in sample size (Hill, 1973; Morris et al., 2014). Expectations generated by the *diet breadth* model of Optimal Foraging Theory (Winterhalder and Smith, 2000; Bird and

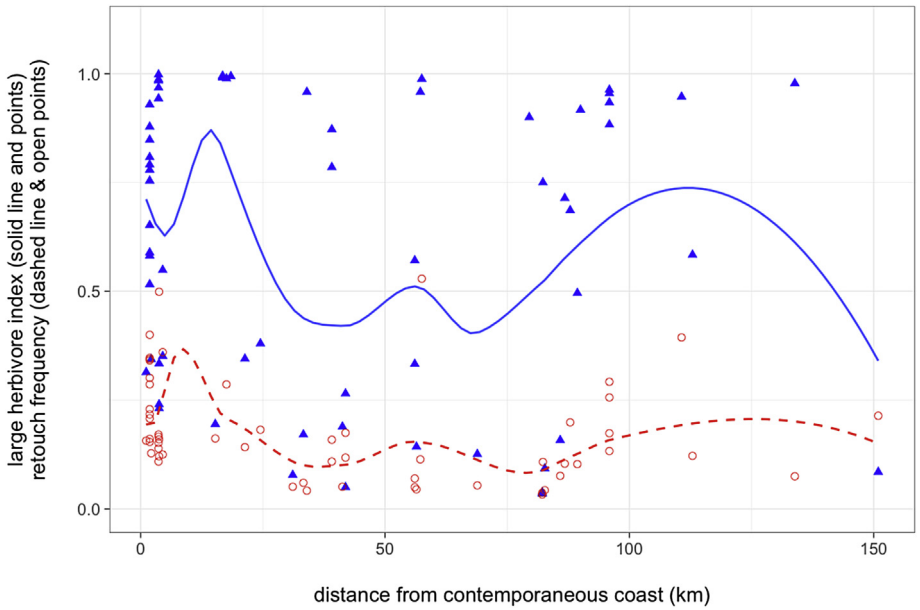

Fig. 10. Spatial patterning in hunting practices (LHI) and land-use (retouch frequency) relative to the shortest (straight line) distance from the contemporaneous coastline for each assemblage. For example, this is the distance to the LGM coast for assemblages dating to the LGM. Blue triangles are assemblages for which LHI could be calculated and blue solid line is a LOESS trend for these assemblages. Red circles are assemblages for which retouch frequency could be calculated, and red dashed line is the associated LOESS trend. Shortest distance to coast calculated in GRASS GIS. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

O'Connell, 2006) are that increasing focus on large game (i.e., food in large packages of high quality calories) should normally be accompanied by lower diet diversity; conversely increased diet diversity should be associated with greater reliance on small game (Rillardon and Brugal, 2014). However, when we compare diversity with LHI, a more complex pattern emerges (Fig. 11). Instead of the expected negative relationship between diversity and reliance on large prey, we find a positive relationship up to LHI values of about 0.67. Beyond LHI = 0.67, the expected negative relationship between diet diversity and prey size appears. Additionally, it is clear that most assemblages with LHI = 1.0 appear anomalous relative to other assemblages (see also Fig. 7). It is likely that small animals were not recorded in these assemblages, though we cannot be certain of it. Because of this uncertainty—and the likelihood that some or most of these assemblages are missing counts of small game—we exclude faunal assemblages with LHI = 1.0 from further analysis of faunal diversity and LHI.

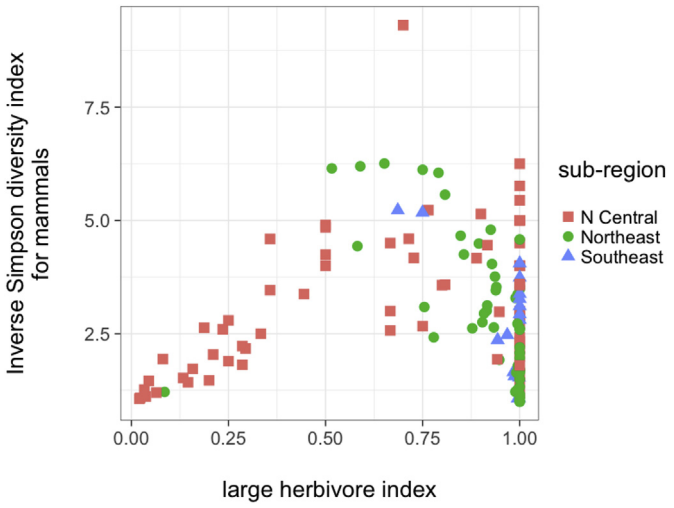

Fig. 11. Diversity, measured by the Inverse Simpson Index, versus LHI for all assemblages with reported counts of faunal taxa. Diversity is calculated only for mammalian taxa because of inconsistencies in recovery and reporting of other vertebrate and invertebrate taxa. Assemblages with LHI = 1.0 are shown here but excluded from Correspondence Analysis shown in Fig. 14.

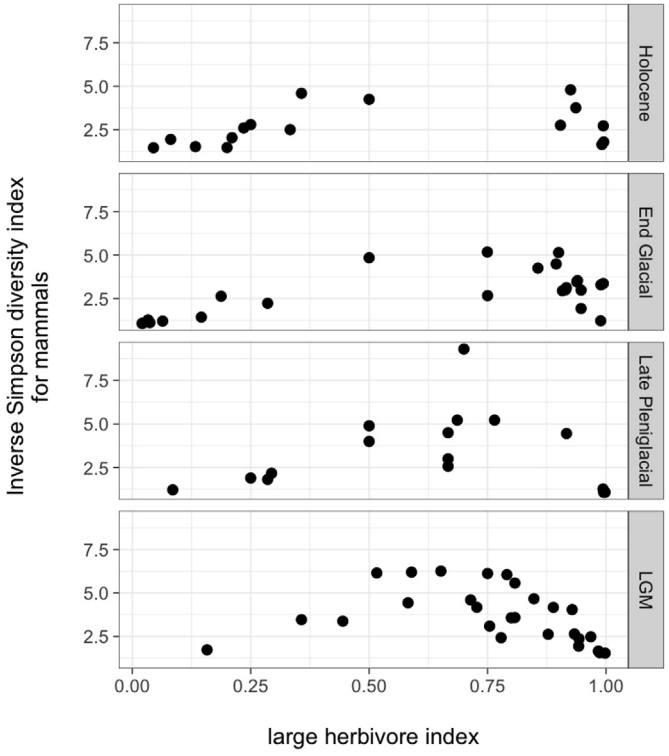

Fig. 12. Diversity, measured by the Inverse Simpson Index, versus LHI for all assemblages with reported counts of faunal taxa divided by time period. See text for discussion.

Decomposing the distribution of Fig. 11 into time periods (Fig. 12) helps in understanding the possible ecological behaviors that generated this overall pattern for LHI and diversity. Over time, assemblages seem to divide into two distinct classes: those in which small game are dominant (LHI<0.3) and which exhibit low faunal diversity (<0.3) and those dominated by large game, where diversity is negatively correlated with reliance on large fauna as predicted by Optimal Foraging Theory models. This increasing differentiation of assemblages also can be seen clearly in Fig. 13. The relationships between retouch frequency and LHI (Fig. 7) suggest that over time, as environmental uncertainty increased in the late Pleistocene, sites were more exclusively occupied either as logistical base camps or specialized targeted resource extraction camps (probably hunting camps in this case). When this temporal trend is merged across all assemblages and periods, it produces the distribution seen in Fig. 11.

We use Correspondence Analysis (Greenacre, 2007; Nenadic and Greenacre, 2007) to more clearly identify ecologically meaningful grouping of faunal taxa and the associations between taxa and archaeological assemblages that accumulated at different periods. Correspondence Analysis (CA) is particularly helpful in this regard because it allows both rows (assemblages here) and columns (faunal taxa) of a dataset to be grouped and viewed along the same derived principal inertia dimensions (analogous to principal coordinates in a principal component analysis). Because no assemblages with complete faunal counts were available for the Southwest subregion, and all assemblages in the Northeast and Southeast subregions except one (Arene Candide) exhibit anomalously high LHI values, we limited this analysis to only French sites in the North Central subregion with consistently available faunal taxonomic data. We carried out separate Correspondence Analyses with assemblages divided according to the four time periods considered here, and present a separate plot for each period in Fig. 14.

These graphs display the distribution of faunal taxa and assemblages with respect to the two first principal inertia dimensions, which respectively account for 29.5% and 20.4% of the variability in faunal taxa and assemblages. The size of the circles (faunal taxa) indicate the importance of the associated taxon to the principal coordinate calculations and the color of triangles marking assemblages is shaded by Inverse Simpson diversity values.

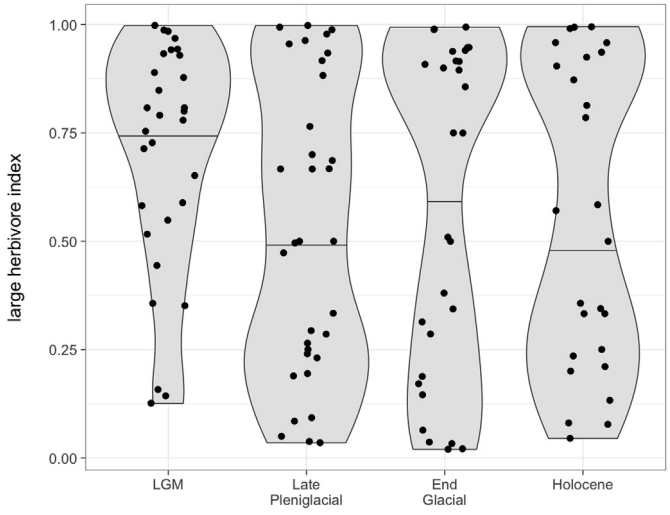

Fig. 13. Violin plots (analogous to vertically oriented density plots or histograms) for LHI by time period. Horizontal lines in each violin plot indicates the median for each group of assemblages.

Herbivore taxa are distributed along CA dimension 1 primarily according to size—especially for those with the greatest contributions to the dimensionality—with the largest herbivores to the right and smallest herbivores to the left. CA dimension 2 seems mainly associated with habitat, with the most important forest herbivores having the smallest values (toward bottoms of the graphs), the most important open country herbivores having larger values, and tundra species with the highest values (toward tops of the graphs).

During the LGM, assemblages are distributed across the CA dimensions one and two in an arc that spans small prey through cold steppe; only one assemblage falls into the large prey/forest sector in the lower right. Single, specialized assemblages (low diversity) are found at the three corners of the distribution (large prey from cold steppe, small prey from wooded habitats, and also large forest prey), but most assemblages exhibit higher faunal diversity, with an emphasis on large game from open environments. This pattern also can be seen region-wide in Figs. 12 and 13, albeit less clearly. In the Late Pleniglacial, assemblages cluster in the middle of the analytical space, again spanning small to large game but with much less focus on (but still use of) open landscapes. Also, assemblages are less diverse than those dating to the LGM. By the End Glacial, assemblages have moved entirely into the arc exploiting forest/woodland environments. There are more assemblages indicating hunting of a wider diversity of (mostly large) prey than in the Late Pleniglacial, but also clear specialization toward both ends of the prey size spectrum—especially for small prey. Finally, in the Initial Holocene, there are a group of tightly clustered assemblages dominated by small game and very low diversity. A second group of assemblages have more diverse remains of large, forest taxa.

Overall, the Correspondence Analysis indicates shifts in hunting practices across the changing environments of the late Pleistocene and early Holocene in the North Central subregion. In the LGM, hunter-gatherers ranged across wooded to cold steppe habitats, opportunistically capturing a wide variety of prey taxa and sizes. During subsequent periods of greater environmental uncertainty, human groups responded by becoming more selective in targeting specific prey at specific locales, with individual assemblages at different sites accumulating much lower diversity of faunal remains.

During the Late Pleniglacial especially, there seems more focus on ecotonal habitats that could allow hunters to target different prey (possibly at different seasons?). We do not have the data to say whether this was more a change in the way humans used the Late Pleniglacial landscape, or a geographic expansion of ecotonal habitats at this time. Lithic evidence from other assemblages from the North Central subregion (Fig. 9) indicates an increase in mobility and ephemeral occupations at this time.

The End Glacial exhibits the lowest precipitation and greatest environmental uncertainty of all periods in the North Central subregion (Fig. 6), but faunal exploitation patterns revealed by the Correspondence Analysis are very similar to those of the early Holocene which experiences warmer, wetter, and much more stable environments. Both periods show a cluster of assemblages in which small prey dominate low diversity fauna. Most likely these are base camps, rather than specialized rabbit hunting sites, where local large game has been depleted and large animals taken at more distant hunting camps are field butchered so that very few bones of these animals are found at base camps. Hunting of large animals takes place only in forested habitats and is opportunistic, especially during the Holocene, producing diverse faunal accumulations at sites. Given that these low diversity, small-prey dominated base camps appear during a time of high environmental uncertainty and continue into a much more stable period, they may be an indication of the ecological impact of increasingly sophisticated and efficient

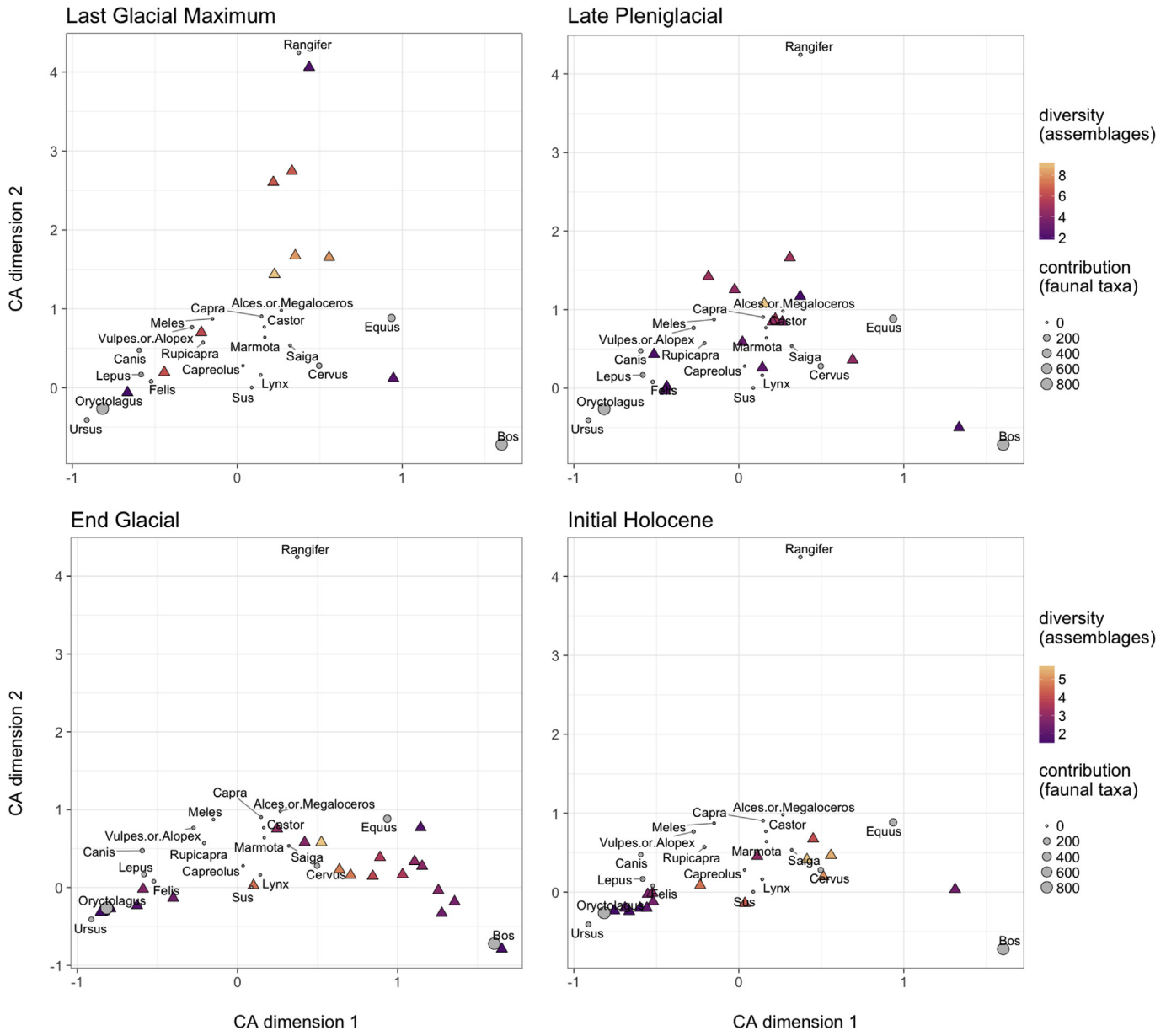

Fig. 14. Correspondence Analysis of faunal assemblages from the North Central subregion. See text for discussion.

hunting practices, beginning in the Late Pleniglacial. Logistical land-use would lead to impoverishment of fauna around base camps and encourage greater dependence on ever more distant, hunting forays to support base camp populations—especially during times of environmental stress due to climate change. We can further speculate that efficient hunting in the extended hinterlands of base camp made forays targeting specific taxa (as seen in the Late Pleniglacial) less reliable over time, encouraging increased opportunism in specialized hunting seen in the End Glacial and even more markedly in the Initial Holocene.

3.4. Demographic change

For the last two decades, summed calibrated date probability distributions (SCDPD, or summed probability distributions, SPD) have been used with increasing sophistication as a proxy for demographic or occupational intensity changes (Shennan and Edinborough, 2007; Williams, 2012; Shennan et al., 2013; Bernabeu Aubán et al., 2016; Downey et al., 2016; García Puchol et al., 2017). While a number of sampling, taphonomic, and statistical considerations can affect the reliability of SPD analyses (Williams, 2012; Contreras and Meadows, 2014), this approach remains a considerably more robust and transparent proxy for prehistoric demographic change than any other method currently available. We combined dates from assemblages used in this meta-analysis with comparable information extracted from radiocarbon databases compiled for the European Pleistocene and Holocene and maintained by Vermeersch at the Department of Geography at the Katholieke Universiteit Leuven (Vermeersch, 2016) and d'Errico and colleagues (d'Errico et al., 2011). This totaled 2386 dates for the LGM through mid-Holocene from the western Mediterranean region. We then merged duplicates and regularized site and provenience names. There are a number of approaches to filtering such a list of dates to improve the reliability of an SPD analysis (Williams,

2012; Timpson et al., 2014; García Puchol et al., 2017). The inconsistent information about the sample, methods, and context of the dates in the public databases precluded applying some of the more robust filtering methods. Nonetheless, we excluded dates with high error values by removing all with CV $\geq$ 0.05, and merged multiple dates from the same proveniences within sites. This reduced the original set to 815 uncalibrated radiocarbon dates (see also Supplementary Information S1). We then used the *Bchron* package for R (Parnell et al., 2011) to generate SPD curves with a non-parametric phase model that fits a full Bayesian Gaussian mixture mode to the uncalibrated radiocarbon data.

Results of the SPD analyses are shown in Fig. 15A (for the entire western Mediterranean region) and Fig. 16A–D (for each of the subregions discussed here). As a simple sanity check, we also compared the SPD curve for the western Mediterranean with the frequency distribution of unique proveniences scaled to the length of time in each of the four periods discussed here (Fig. 15B). Although at a much coarser-grained temporal resolution, the frequency distribution of archaeological proveniences is broadly consistent with the shape of the SPD curve. We should note in this respect that it is generally recognized that taphonomic processes will lead to underrepresentation of older time period relative to more recent ones in SPD curves (Williams, 2012). Indeed, in stratified cave/shelter locales that make up the overwhelming bulk of Paleolithic sites from which our dates are drawn, LGM levels are often buried below meters of later deposits, and are thus exposed in much smaller areas. Moreover, the need for larger samples of organic material to return finite dates, even with AMS methods, and the taphonomic loss of datable material from more ancient contexts, potentially combine to further reduce the number of dates available for this period. We do not attempt to mathematically correct for this admitted bias (e.g., Williams, 2012), but simply note that the lower density values for the LGM may be in part a function of these issues. Likewise, the precipitous decline in most recent end (right side) of the SPD curve in the Holocene is a statistical artifact of our study which only examines assemblages up to 6000 cal BP.

Comparison with paleoclimate proxies is informative and relevant to the analytical goals of this study. In Fig. 15A, we superimpose rescaled LOESS trend lines for delta ^{18}O from the GISP2 and NGRIP2 ice cores shown in Fig. 1. Although drawn from completely independent datasets, the main fluctuations from the ice core data closely match those of the SPD curve, with a slight time lag for the human response (or a consequence of how ages for the ice core data were calibrated). Given the other evidence presented above, the fluctuations in the SPD curve seem to reflect real changes in occupational intensity and possibly population density in response

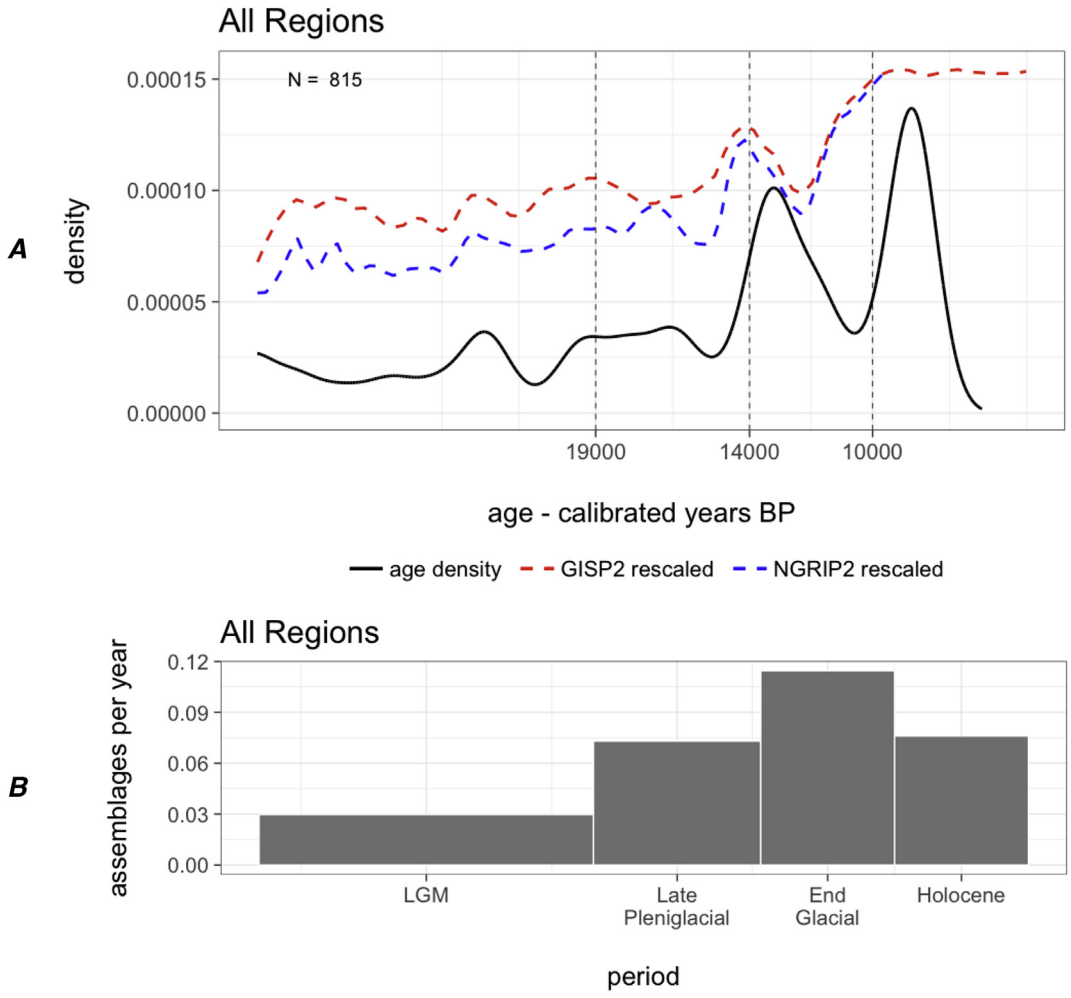

Fig. 15. A) Summed probability distributions (SPD), or summed calibrated date probability distributions (SCDPD) calculated from radiocarbon dates in the western Mediterranean region (heavy black line). Dashed lines are the LOESS trends for delta ^{18}O values from Greenland ice cores shown in Fig. 1, rescaled to fit on SPD y axis. Vertical dashed lines mark the four time periods used here. See text for discussion. B) Assemblages used for SPD analysis, scaled as assemblages/year within each of the four time periods used in this paper (LGM = 10ka, Late Pleniglacial = 5ka, End Glacial = 4ka, Initial Holocene = 4ka).

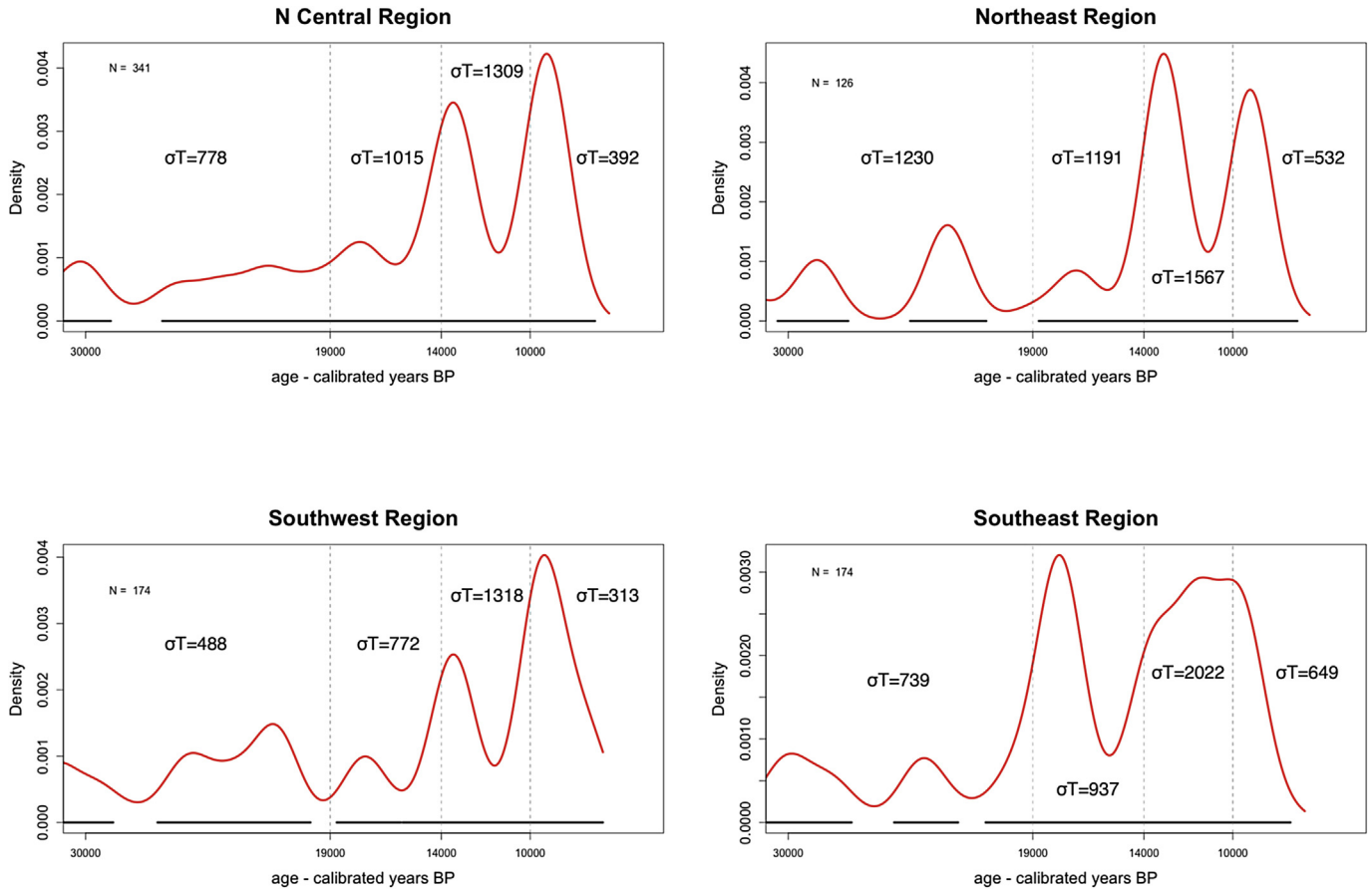

Fig. 16. SPD curves for each of the four subregions. Variance in annual temperature for each of the four periods (from Fig. 6) shown for reference.

to the regional manifestation of global climate changes.

In Fig. 16, the SPD curves for each of the four subregions examined here show clear regional differences in human demographic response to environmental changes. Several general observations can be made. One is that across all four subregions, the greatest demographic oscillations occur during the Late Pleniglacial and End Glacial, the periods identified as experiencing the greatest environmental uncertainty in this region. Especially apparent is the sharp rise in the SPD curves at the Bølling-Allerød Interstadial, and the strong drop in the curves of all subregions except the Southeast coterminous with the Younger Dryas. The LGM, by comparison, seems overall more stable demographically (North Central subregion) or displays a relative demographic high (other three subregions). In Italy, low values of the SPD curve for the Northeast subregion for the Late Pleniglacial corresponds with a steep rise in the curve of the Southeast subregion during the same interval. The SPD curve also remains high for the Younger Dryas in the Southeast subregion, while the Northeast sees a precipitous drop. This raises the question of whether we are seeing population shifts from northern Italy into peninsular Italy and associated islands during these periods. Corresponding shifts are not seen between the Southwest and North Central subregions.

4. Discussion and conclusions

Unlike modern people, almost all of whom live in sedentary communities and over half of whom are urban dwellers, hunter-gatherers occupy entire landscapes, not specific locales. The camps that occasionally become archaeological sites, like different rooms in the houses of sedentary modern people, represent only a few slices of hunter-gatherer life, with a bias for archaeological preservation in caves and rockshelters that may well not be very representative of those lives (Barton and Clark, 1993). If we are to gain better insight into how our hunter-gatherer ancestors managed to survive—and ultimately thrive—in the face of significant environmental change, uncertainty, and risk it is imperative that we attempt to take a regional perspective on human ecology that corresponds to the regional context in which their lives played out. We have attempted to illustrate how such a regional meta-analysis can be done using the western Mediterranean and the transition from full glacial to full interglacial as a case study. This could only be accomplished by synthesizing the results of decades of dedicated archaeological studies, each of which provides detailed information about a tiny window into a regional whole for prehistoric human ecology. We have also synthesized diverse paleoecological data that provide the environmental context for human ecology. Efforts to paint a regional picture of prehistoric systems by synthesizing results of numerous individual studies are not a new approach, of course (e.g., Villaverde et al., 1998; Gamble and Gamble, 1999; Cacho Quesada et al., 2011; d'Errico and Stringer, 2011 and numerous edited volumes). These studies have attempted to create a synthetic narrative from the narratives and interpretations of multiple individual studies. Our approach differs in that we have carried out new analyses on the combined datasets of many individual studies, providing opportunities for new insights about past systems beyond those offered by the original excavators. What can we say, then, from this kind of regional meta-analysis integrating information from hundreds of assemblages and over

half a million artifacts, spanning over 20,000 years of human prehistory across the western Mediterranean region?

The LGM was a long interval exhibiting the greatest environmental stability of the end-Pleistocene until the onset of full interglacial conditions in the early Holocene. Across the western Mediterranean, the LGM displays greater environmental predictability geographically and on inter-annual time scales than even the mid-Holocene. During the LGM, western Mediterranean human groups were quintessential ice age hunters, well adapted to the more open landscapes of full glacial Europe, and accumulating faunal assemblages dominated by large game at their camps. Land-use was organized around logistical mobility, unsurprisingly since this kind of organization is most common among high latitude hunter-gatherers described in the ethnographic literature. While bones of small prey are found at likely base camps, there are also bones of larger herbivores in assemblages from these contexts. Human populations seem to have been demographically stable during this 8000–10000 year interval, with notable increases in all but the North Central subregion (possibly more significant than they appear due to taphonomic bias against older radiocarbon dates).

The transition from glacial to interglacial conditions was ecologically traumatic, on the other hand. This interval is characterized by high decadal-scale variance in temperature and precipitation compared with the LGM and mid-Holocene. Unfortunately, we do not have paleoclimatic models with sufficiently fine spatial resolution to also assess spatial predictability for this transition period. Pleistocene hunter-gatherers responded to environmental change and increased uncertainty through land-use strategies, hunting practices, and demographic shifts. With respect to land-use, there is an increase in assemblages from ephemeral occupations, especially in the northern two subregions. In the Northeast subregion, this shift is manifest in the rarity of assemblages that can be ascribed to base camp occupations. This could indicate a shift from primarily logistical to residential mobility, though this seems unlikely given other evidence from the region. Missing base camps also could be under the modern Adriatic, much of which was dry land during glacial times, but there are clear base camps in this subregion during the LGM, when even more of the Adriatic bottom was exposed.

At a regional scale, there is increasing differentiation between base camps in which small prey increasingly dominate faunal assemblages (see also Aura Tortosa et al., 2002), and ephemeral hunting camps with remains of large herbivores. This may have been the result of feedbacks between overhunting of large prey in the vicinity of more intensively occupied base camps, coupled with climate-induced environmental stress on animal populations, generating increased pressure to range farther in search of large prey which were field butchered (with mostly boneless meat returned to base camps). Associated with this, ephemeral hunting camps suggest opportunistic hunting of whatever large herbivores could be found by the End Glacial. Consistent with these observations, the period between the LGM and Holocene interglacial sees significant elaboration of hunting technologies, including the appearance of spear throwers, complex compound weapons, harpoons, and fish hooks/gorgets. Many of these weapons require more manufacturing time in longer-occupied base camps and are increasingly portable for carrying on long distance hunting forays. This pattern continues and intensifies into the Holocene, somewhat at odds with the widely accepted view of Epipaleolithic and Mesolithic groups as broad-spectrum foragers (see also Rillardon and Brugal, 2014). Such highly logistical land-use would have help preadapt western Mediterranean hunter-gatherers to the increased sedentism that accompanied Neolithic economies a few millennia later.

Human demography undergoes dramatic oscillations during the Late Pleniglacial and End Glacial, with a possibility of significant north-south population translocations in Italy. At resolution of the SPD analyses, however, human demography seems to be responding more to the larger-scale, rapid shifts in global climate (e.g., the Bølling-Allerød and Younger Dryas) than overall changes in uncertainty and risk.

This raises the possibility that culturally-mediated adjustments to SETS give them sufficient resiliency to adapt to significant changes in environmental uncertainty … up to a point. Past some threshold, exemplified by the Younger Dryas here, social and technological adaptations are insufficient to forestall regime shifts in SETS with significant demographic consequences. At this general level, the evidence from the prehistoric western Mediterranean is consistent with other studies of regime change in other contexts (Scheffer and Carpenter, 2003; Alessa et al., 2008; Scheffer et al., 2012; Downey et al., 2016), and offers insight into resilience and tipping points in human SETS. Understanding how previously successful human populations were affected by regional-scale consequences of global climate change across the glacial/interglacial transition can help us better anticipate potential impacts of anthropogenic climate change on modern human societies. Globally, even more 'radical' responses of human SETS to the environmental uncertainty and ecological risk of the glacial/interglacial transition included taking increasing control of local ecosystems through management of reproduction, competition, and even genetics of important plants and animals—strategies that led in some places to the agro-ecosystems that subsequently took over the world.

Overall, this meta-analysis has been largely descriptive, focusing multiple lines of evidence more on *what, when,* and *where* questions than *how* or *why*. To the extent that we have proposed mechanisms that drove changes in human SETS, they are best considered hypotheses that will require future testing. Isaac Newton famously wrote, “If I have seen further it is by standing on the shoulders of giants.” Research like the meta-analysis presented here must build on the work of others. The Paleolithic of the western Mediterranean has been studied intensively for nearly two centuries, and the 122 sites from which we have compiled data represent only a fraction of the many hundreds of Pleistocene and early Holocene locales that have been excavated in this region. Nevertheless, while fieldwork is a fundamental component of archaeological practice, excavations at individual sites are such tiny, fortuitous windows on the past that, by themselves, they provide little information about the operation and evolution of social-ecological-technological systems that make humanity so unique and so fascinating to study. It is only when we combine the information from a sufficient number of these miniature portals can be begin to build credible knowledge of human systems—knowledge that provides us better insight into human prehistory and which can be applied to understanding human systems dynamics today.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.quascirev.2017.09.015.

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